QUANTITATIVE ENTOMOLOGY.

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The best answer to the question, "What is it that we consider worth while in Entomology," is given by the record of our activities. There are innumerable descriptions of rare new species of insects. Peculiar habits or structures receive detailed consideration. Unusual inter-relationships between insects and their environment compel our attention and interest. An insect that is noticed for the first time to attack our crops or our persons is investigated with great thoroughness.

When we make textbooks we endeavor to assemble and arrange in an orderly fashion this wonderful wealth of detail. Throughout the exceptional, the unique and the unexpected are given the emphasis. All of this is right and proper. It is in this way that all sciences have been developed, but this does not constitute the final goal nor leading method of science. Finally, the predominating question becomes not what, but how much? Finally, it is a question of values. Thus in physics we have ceased to give much prominence to the mere operation of physical laws, but must measure the results with such accuracy that this science has almost become a branch of mathematics. Likewise in chemistry the wonderful advances of the subject in later years both in theoretical and technical lines depend upon the study of reactions quantitatively.

The present paper is intended as suggestions and a plea for the development of a quantitative entomology. Qualitative work must not cease nor be abated, but to it should be added the higher development of the subject which will finally come to be considered the essential portion of the science.

A beginning has already been made in nearly every department of entomology towards this quantitative method of study, enough to give us some idea of the simpler lines of procedure and of the results likely to be secured. Quantitative entomology is not therefore a wholly new idea, but is a great territory, the boundaries only of which have been explored and in the depths of which we may expect to find the chief justification for our endeavors. Entomology is now confronted with the same condition which older sciences experienced and like them must become an exact science if it is to realize its highest development.

Along with the improvement in accuracy and detail there must come at the same time a simplification through the elimination of the non-significant details of each department of entomology and a clearer recognition of the distinctness of these departments.

DIAGNOSTIC ENTOMOLOGY.

In no place is this need more clearly shown than in what we know as Systematic Entomology, a very utilitarian department concerned in the assigning of names to insects and in providing the means whereby these insects may be identified. Such an entomologist is a Diagnostician. His problems are numerous and difficult enough, requiring the specialization into very restricted groups, and is rendered more difficult by the fact that many have confused their work with two very different departments — classification and descriptive entomology.

Keys have been rendered unnecessarily difficult by attempts to make them conform in arrangement to supposed phyletic sequences and pages of descriptive matter in defining a new species seldom results in making its correct identification more certain and certainly makes it much more laborious.

Keys should be arranged in a manner to best facilitate identification, every other consideration should be subordinated to this end. This principle appears to be beyond controversy. How it shall be applied, that is, what form tables will finally take, is a matter that time will decide.

Two plans of arrangement are presented for your consideration, one based on dominance and the other on historic sequence.*

The latter appears to be best for the species of a genus where the commoner forms are liable to be first described and the former method for larger groups which, because of the changing views as to what they include, can be best studied according to their present rather than their historic content. Keys constructed along these lines have proven remarkably simple and workable. They are particularly good for teaching

^{*} The paper was illustrated at this point by the keys given in the author's "Families of Insects," and "Insects of California."

purposes, since they emphasize the dominant groups and their most evident characteristics. Keys can be wisely restricted to single characters wherever possible and the use of "usually" or "rarely" in connection with a character should be rigorously excluded. Key characters should be so selected that the differentiation is most certain and evident. All differentiating characters must be definite degrees of variation.

The diagnosis of a species should be limited to differentiating characters. A great deal that finds its way into the description of a new species is descriptive and not diagnostic and is worse than useless for the purpose of identification. On the other hand, very few descriptions are exhaustive enough. Every character that rightfully belongs in the diagnosis of one species of a genus should appear in the diagnosis of every other species of that genus and each genus will have its own set of differentiating characters.

The contention is, first, that there exists in each genus a set of definite quantitatively measurable variants which constitute the diagnostic resources for that genus and that all of them should be included in each specific description, but that a distinction should be made between them for use in keys, only those most evident or tangible being employed and that the key should be arranged solely for convenience in identification.

DESCRIPTIVE ENTOMOLOGY.

What we know as the specific descriptions of insects even in their most elaborate form are too meagre to be looked upon as fairly representing what descriptive entomology should accomplish.

For a few insects the accounts of the structure that have been published are perhaps sufficiently voluminous, but only the beginning has been made in the approach to the ideal which I wish to urge as the goal for future work.

Descriptive Entomology is concerned with, 1st, a study of size and form; 2nd, surface differentiation; 3rd, color and pattern and 4th, internal structure.

Size and Form should be so studied as to become expressible in terms of the dynamics of growth. We must discover and measure the intensity of the determining factors. A few categories are already well known. We have, for instance, (a) cases where there appears to be a simple difference in the size of all parts simultaneously, (b) cases where in the ontogeny of an insect certain parts gain their growth at a different period than others and the conditions affecting general size may show most prominently in these organs and (c) cases where the tendency to abnormal growth seems limited to certain organs and the adjacent parts profit or suffer through this abnormality.

This list of categories will have to be enlarged and subdivided as investigations will show necessary until we can recognize the nature of the variation in the growth of organs or portions of the body that brings about all the differences we observe in size and form.

Surface differentiations result from variations in the secretion of cuticle by the individual epithelial cells and should be expressed in terms of these activities. Often a very definite relationship between the surface modifications and the form of the parts of the body may be recognized. The most evident categories are (a) where the cells over the whole sclerite or specialized organ produce a homogeneous cuticle, (b) where an equally definite relationship exists but with bordering or concentric specializations, (c) where the structural modification has relation to general body structure rather than to individual sclerites and (d) where the modification conforms to an internal structure, particularly muscle attachments.

The qualities of the surface modifications we express by a large series of Latin adjectives describing the mass effect of these cuticular differentiations. These adjectives should be redefined in terms of their ultimate structure in the individual cells and subdivided as found necessary where the same superficial appearance is the result of essentially different modifications.

The accurate quantitative statement of surface structure will become possible as soon as progress is made in the more logical study of the topographic and qualitative differentiation just suggested.

Color and pattern, like surface structure must be studied as the resultant from the activities of individual cells, but is not wholly a question of pigment as has already been amply shown nor wholly of epithelial activity. Our classification

and nomenclature of colors require an entire reorganization. They should be primarily based on the nature of the color reflecting substance rather than on the physiological effect of the light rays that are most evident to the eye. This is necessary before we can make any progress in a quantitative statement of color values. The topographic differentiations or patterns are subject to the same classification that have been indicated for the surface modifications and doubtless are often responses to the same phylogenetic or ontogenetic causes.

Internal structure may be divided into two chief divisions, the larger portion of the muscular and nervous systems whose specialization is definitely associated with details of the external structure and the remaining tissues associated with vegetative functions.

The former should be considered in connection with the skeletal parts with which they are associated and their differences in histological structure and in shape and size studied in relation to their functional requirements. When the study is carried far enough to differentiate the various types of structure there will remain the ultimate distinctions to be made by quantitative determinations.

The vegetative functions, digestion, respiration, circulation, excretion and reproduction, involve a series of structures having a more remote connection with the external environment, but nevertheless, find their best basis of classification in the effect of the external world on their individual activities, and, of course, involves a full comprehension of the details of their physiology and has relatively little to do with the external topography except in its general aspects.

All structures according to the conception here promulgated are classifiable into groups comparable with genera and species, the former distinguishable by differences of kind, the latter by differences of quantity. That descriptive entomology has before it the task of perfecting its nomenclature so as to be able to describe all differences of kind explicitly and accurately and then, by quantitative determinations can give exact descriptions of insect structure, a description which expresses the nature and character of the parts rather than their superficial appearance.

CLASSIFICATION.

The classification of organic beings has to do with questions of phylogeny exclusively. No small amount of confusion has arisen from attempts to combine classifications and keys for identification to the detriment of both. The groups recognized by both the Diagnostician and the Systematist should be the same, but the characters and arrangement need have nothing in common. The best diagnostic characters may have little or no phyletic significance and the phylogenetic sequence of groups may introduce confusion and difficulties in identification.

The problems of phylogeny are two, the derivation of groups and the coordination of groups.

Derivation of groups to determine by a comparative study of the structure, substantiated wherever possible by the historic sequence of the first appearance of the groups as shown by the geological record, the underlying principle being that the complex structure was derived by the specialization of simple structures. Two groups are supposed to have a common ancestor if they resemble each other in most of their characters. The characters by which they differ are supposed to be those historically responsible for the separation of the groups. As a matter of fact groups are usually distinguishable by numerous characters, many of which are accidental or only incidentally coordinated with the historic basis of the segregation. The Systematist therefore, must search for the differentiating character, which may be internal or difficult of observation and very unsatisfactory for diagnosis, but the only one perhaps that gives a clue to the causes which brought about the separation of the groups. Differentiating characters are perhaps always differences of kind, representing alternative possibilities in growth and either a new structure in the place of an older one, or progress in the development of a structure of which there may be two possible lines of growth. Some differentiations involve no appreciable change in other parts of the body, while others are revolutionary. The former we conceive may frequently recur, giving us examples of parallel development. Many generic differences are clearly of this character. The more involved modifications give so many opportunities for variation that strict parallelism appears to be impossible.

Thus the production of wings is a specialization least liable to have occurred more than once in the history of insects, while the suppression of wings is an often recurrent phenomenon.

Again characters which are of themselves of little moment may open the way to other reorganizations of structure of highest significance. This development of complex metamorphosis may easily have occurred more than once. The male Coccidæ probably have such a mode of development following the most strict definition of the process and the hypermetamorphosis of Meloids is a further extension of practically the same kind of specialization, but the development of this mode of growth opened the way to the origin of the four largest orders.

To properly estimate the relative phylogenetic significance of characters all of these considerations must be comprehended in our classification. From this point of view no character is important in itself only in its relation to the whole organization of the members of the group.

Coordination of groups consists of determining which are to be considered of equal rank. This is a subject upon which there has been, and still is, two very definite tendencies. Entomologists are in most complete accord for instance as to the orders into which perhaps $95_{0}^{\prime\prime}$ of the species of insects belong and nevertheless, the current text books vary from 7 to 37 orders. The same tendency is seen among systematists in every group of plants and animals.

Some naturalists may have the conception that every group sprang from a single mutant pair and from the time of their mutation the new group existed. The Lepidoptera are for instance derived by common consent, from the Trichoptera, because chiefly of the almost complete conformity of the venation of certain members of the two groups, but there are at least two very different types of wings in which this perfect conformity is seen which are most easily explained by the assumption of a tendency of development seen in a series of species in one order giving rise to a series of forms in the new group in the same manner as most conceive that geographic isolation may bring about two species with parallel varieties. The variations being parallel because residual.

If this principle is accepted, as most naturalists do, the necessity of making quantitative valuations to the amount of variation separating groups is necessary. The traditional primary classification of insects is represented by the common names and was adapted by Linnaeus for his orders. In these the quality of variation is represented by the differences between bees, flies, butterflies and beetles. The practical question to be settled is whether the difference between, say an ant lion and a sialid, is of the same order of magnitude. It would seem that those who have gone to the extreme in increasing the number of orders have either ignored or rejected this principle. After wings were produced we must conceive that there was a single order, family, genus and species, that first there occurred a multiplication of species, some of which became more, and, finally, were generically different, and last of all the difference of the most remote forms represented different orders. The differences between the Orthoptera and Neuroptera most probably represents the progressive development of a whole family, rather than a great mutation of a single species and that historically there was a period where two families representing the two orders were families of the same order. A time is reached when the differences become great enough to be of ordinal value.

We must strive toward the goal where we can assign a quantitative degree of differentiation as representing family rank and another for order rank, etc. to replace our present plan of making such groups on the basis of indefinite mental impressions.

DISTRIBUTION.

Most collectors of insects are very careful to have the locality and date with every specimen appreciating that the geographical and seasonal distribution of insects are questions of great importance. The data accumulated in this way is of very unequal value, because in some cases the absence of record indicates the absence of the species from a locality and in other cases may indicate the rarity of the insect. The biologic significance of an insect depends on its degree of abundance. The real importance of the subject will lie in accumulating data to show the part each species plays.

There are over 10,000 species of insects recorded in California. Of these not over 1000 are found in many collections or known from any large numbers of localities. In none of the 9000 is there sufficient data at hand or liable to be secured to assist in solving any of the problems of geographical distribution. Nor do any of them play any important part in biological problems, unless it be the problem connected with the maintenance of existence by rare species.

If only in the neighborhood of 10% of the insects contributed much to our knowledge of distribution it is probable that 1%includes all those whose abundance causes them to play an important part in the ecological relationships or in economics.

We must devise means of expressing the dominance of species perhaps in terms of their relative frequence of individuals or relative mass and for ecological purposes it might be better expressed in terms of food consumption as related to its distribution in regions, in special habitats or in seasons. The idea is that we have only touched some of the exterior details on the surface of the subject and must develop means of studying the quantitative significance of distribution in order to arrive at the real meaning of the subject.

But it will not be necessary to follow this idea through all the departments of entomology to the study of Physiology, Development or Life History, adaptations and the various other departments of ecological study. One will see at once that the same need of a definition of the elements of the subjects, their subdivision and classification until we can express differences quantitatively with quite rigorous accuracy will open the way to a new and loftier conception of our subject and in conclusion I wish to point out some of the changes this line of development is beginning to produce in economic entomology and particularly to the portion which might be called Horticultural Entomology.

Economic Entomology has gone through remarkable changes of viewpoint. Half a century ago the subject would have been defined as the study of injurious insects. After the remarkable series of discoveries in the seventies and eighties of our whole series of efficient insecticides, the thought of entomologists so changed that the subject might have been defined as treating of the methods of killing injurious insects. Now the emphasis is shifting to the truer conception that economic entomology is the science treating of the methods of making money by the control of insects. The older entomologist devoted a great deal of time to life histories, parasites and predaceous insects. After really effective insecticides were discovered these so-called natural remedies were chiefly relegated to those injurious species not satisfactorily handled by real remedies and finally we are beginning to appreciate that even the knowledge of an effective way to kill an insect pest is not enough to bring it within the domains of a truly economic entomology, it is only those things we can do at a profit with which economic entomologists are, or should be, concerned.



This changing attitude does not yet find full expression in our books and, I am convinced, in our teaching. We are giving too much emphasis to minor matters. On the accompanying chart are given the relative economic importance of insects in California as based on the best means we have at hand of measuring this relationship, that of the money expended in control work. We spend about a million dollars a year in this work in California, divided approximately as shown in the chart. Some items may have only a temporary status in the rank shown, such as the Citricola scale and Thrips, but in the main features this chart will probably represent the situation for years to come. Our books on economic entomology give about 5% of their attention to the nine insects that constitute 95% of the control work.

This emphasizes in a striking manner the prominence we gave to the occasional and exceptional matters which will come to take more nearly their proper place when this tendency towards quantitative work has progressed further.

I trust while those present may not be ready to adopt all or any of the suggestions of this paper that the underlying idea will meet with your approbation and that perhaps some may be stimulated to take what is here urged as the future progressive work along the lines in which the trend of the science must proceed.